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Multi-scale habitat selection of key frugivores predicts large-seeded tree recruitment in tropical forest restoration

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Abstract. Large-seeded, animal-dispersed (LSAD) trees include some of the most valuable and threatened species in the tropics, but they are chronically underrepresented in regenerating forests. Toucans disperse many LSAD species, so attracting toucans to regenerating forests should help re-establish more diverse tree communities. We ask: (1) What constitutes suitable toucan habitat in premontane southern Costa Rica? (2) How much do small-scale restoration strategies influence toucan visitation compared to landscape-scale habitat suitability outside of restoration sites? (3) How well does toucan visitation predict the richness of LSAD tree species recruiting into regenerating forests? We combined habitat suitability models with long-term toucan observations and comprehensive tree recruitment surveys to assess these questions in a multi-site forest restoration experiment. Restoration treatments included tree plantations, natural regeneration, and applied nucleation. Habitat suitability obtained by modeling for three sympatric toucan species was predicted by elevation and the extent and age of landscape forest cover. Within suitable landscapes, toucans visited areas restored via tree planting ≥5 yr sooner and ≥2× more often than plots restored via natural regeneration. Tree plantations in suitable toucan habitat at the landscape scale had LSAD tree recruitment communities that were 2–3× richer in species than plantations in poor toucan habitat, and 71% (15/21) of all recruiting LSAD tree species were found only in plantations where landscape habitat was suitable for the largest toucan, *Ramphastos ambiguus*. Results support a multi-spatial-scale model for predicting toucan-mediated dispersal of LSAD trees. Tree planting increases toucan visitation and LSAD tree recruitment, but only within landscapes that represent suitable toucan habitat. More broadly, habitat suitability modeling for key seed dispersers can help prioritize restoration actions within heterogenous landscapes.

Key words: biodiversity conservation; frugivory; habitat suitability; natural regeneration; secondary forest; seed dispersal; species interaction; tree plantation; zoochory.

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INTRODUCTION

Secondary tropical forests are expected to conserve a substantial portion of terrestrial biodiversity in this century, but many forest-dependent organisms struggle to recolonize degraded habitats (Wright and Muller-Landau 2006, Gibson et al. 2011, Chazdon 2014). An ongoing challenge for tropical forest restoration is to identify these organisms and develop practical methods for facilitating their re-establishment. Large-seeded, animal-dispersed (LSAD) trees represent one such group. LSAD trees include some of the most valuable and threatened tropical species (IUCN 2019), and many are important carbon reservoirs because they grow slowly and have dense wood (Bello et al. 2015), but LSAD trees often fail to recolonize secondary forests due to small, fragmented populations and limited seed dispersal (da Silva and Tabarelli 2000, Reid et al. 2015). Also, LSAD tree seeds can be difficult for seedling nurseries to acquire and expensive for restoration managers to plant, disincentivizing their use in forest restoration (Brancalion et al. 2018, Engert et al. 2020).

Solutions to the LSAD tree recruitment problem fall into two classes based on the mechanism for increasing LSAD tree representation in restored forests. One is to encourage the use of LSAD tree species in restoration plantings by increasing access for seed collectors to protected areas where LSAD trees persist, subsidizing the cost of these trees to planters, or including minimum limits for diversity and abundance of LSAD trees through restoration legislation (Martínez-Garza and Howe 2003, Brancalion and Holl 2015, Brancalion et al. 2018). A second option relies on facilitating animal-mediated restoration of LSAD tree communities by attracting their dispersers to recovering habitats. Attracting LSAD dispersers may be accomplished by prioritizing restoration within certain landscape contexts, such as areas connected to existing populations by stepping stones or corridors (de la Peña-Domene et al. 2016). LSAD dispersers could also be attracted through local strategies, such as planting preferred food plants (Goosem and Tucker 2013, Howe 2016). These two strategies, cost reduction and disperser attraction, should be mutually reinforcing. All

else being equal, re-establishing seed dispersal processes is preferable as it has the potential to increase colonization by many LSAD species and does not require extensive inputs for seed collection and propagation.

Several ecological principles need to be considered in designing restoration strategies that facilitate LSAD tree colonization by attracting seed-dispersing animals. First, large-seeded trees generally are dispersed by large-gaped animals (Wheelwright 1985, Corlett 2017). Animals with small mouths typically do not transport large seeds, although some fruit bats do (Melo et al. 2009). Second, effective seed dispersal requires not only that seeds are dispersed but also that they have a reasonable probability of establishment at the dispersal site (Schupp et al. 2010). Some experimental restoration strategies are aimed at attracting seed-dispersing animals into degraded habitats but fail to address critical barriers to plant establishment (Reid and Holl 2012). It follows that for an animal to be an effective seed dispersal agent for LSAD trees in a restoration context, it must not only remove seeds from source trees but also carry them across non-forested landscapes and deposit them in suitable sites within regenerating habitat (Beltrán and Howe 2020).

Large birds such as toucans and hornbills are likely to be important LSAD dispersers in many tropical forest restorations given their ability to consume large quantities of seeds, their movement capacity and willingness to cross wide gaps between forest habitat, and the high quality of their seed dispersal in terms of seed viability and deposition in suitable sites (Beltrán and Howe 2020). Yet, evaluating the effects of restoration strategies on toucan-mediated seed dispersal has been challenging due to the typically small scale of restoration plots relative to these birds' home range sizes and the associated lack of detections (Robinson 2010, Lindell et al. 2013, Reid et al. 2014). Moreover, most past restoration experiments have been conducted at one or a few sites and hence lack the level of replication and spatial independence needed to evaluate the effects of landscape heterogeneity on LSAD plant disperser visitation. Prior data from our study system in an agricultural landscape with intermediate regional forest cover show that tree

planting increases dispersal and recruitment of LSAD trees (Reid et al. 2015, Holl et al. 2017). A separate study in Mexico demonstrated that LSAD dispersal and recruitment are greatest when tree plantations are well connected to seed sources (de la Peña-Domene et al. 2016).

Here, we combined landscape-scale toucan habitat suitability models with a LSAD tree recruitment survey and long-term toucan observations in a well-replicated forest restoration experiment in southern Costa Rica. We aimed to answer three questions about toucan-mediated seed dispersal in tropical forest restoration. First, what constitutes suitable toucan habitat in our region? Second, how much do small-scale restoration strategies influence toucan visitation compared to landscape-scale habitat suitability outside of restoration sites? Third, how well does toucan visitation predict the richness of LSAD tree species recruiting into regenerating forests? We hypothesized that (1) habitat suitability for three sympatric toucan species would increase with the amount and age of landscape forest cover; (2) local-scale restoration treatments would play a secondary role in concentrating toucan activity provided that sites are located within suitable habitat at the landscape scale; and (3) toucan visitation and habitat suitability would increase the richness of LSAD tree species recruiting into restoration plots.

METHODS

Study area

Our study area was a ca. 500 km² agricultural landscape in the Coto Brus Valley of southern Costa Rica (Fig. 1). The landscape is dominated by small-scale cattle pastures and low-intensity, sun-coffee plantations, with old-growth and secondary forest fragments of varying sizes. The dominant native habitat is transitional between tropical premontane wet forest and rain forest (Holdridge et al. 1971). Forest covered most of the region in 1947, but about two thirds had been cleared by 1980 (Zahawi et al. 2015). By 2014, forest covered ~28% of the study region (Zahawi et al. 2015). Elevations ranged from 800 to 1500 m above sea level. Mean annual rainfall was approximately 3.5–4.0 m/yr with a dry season from December to March, and mean annual temperature was 21°C at the Las Cruces Biological Station (8°47′7″ N, 82°57′32″ W), which is centrally located within the study area.

Experimental restoration design

We selected 11 forest restoration sites established in 2004–2006 on former agricultural lands that had been farmed for ≥18 yr (Holl et al. 2011) (Appendix S1: Table S1). Study sites spanned a deforestation gradient ranging from 13 to 82% tree cover within 1 km and represented a randomized block design. Each site contained three 0.25-ha plots, which were separated from one another by ≥5 m. Plots were randomly assigned one of three experimental treatments: (1) natural regeneration, (2) applied nucleation, or (3) plantation (Appendix S1: Fig. S1). Natural regeneration plots were left to recover without tree planting. Applied nucleation plots were planted with six patches of tree seedlings (86 seedlings/plot). Plantations were planted with rows of tree seedlings throughout (313 seedlings/plot). All plots were fenced to prevent cattle incursion and were hand-cleared with machete for 2.5 yr. Study sites were separated from one another by ≥0.7 km.

Tree seedlings planted in applied nucleation and plantation plots consisted of two widely planted native species, *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized legumes, *Inga edulis* and *Erythrina poeppigiana* (both Fabaceae). *Inga* produces an indehiscent fruit with an edible pulp that is consumed by primates, *Terminalia* and *Vochysia* produce winged seeds adapted for wind dispersal, and *Erythrina* produces brown seeds with no obvious dispersal mechanism. None of the planted tree species produce fruits regularly eaten by toucans.

Focal avian LSAD dispersers

Among several groups of large-bodied (>100 g) fruit-eating birds in southern Costa Rica (Appendix S1: Table S2), we investigated the three toucan species (Piciformes, Ramphastidae) that occur in the region: *Aulacorhynchus prasinus*, *Pteroglossus frantzii*, and *Ramphastos ambiguus* ssp. *swainsonii*. Toucans are consistently important seed dispersers for a variety of neotropical trees (e.g., Howe et al. 1985, Rother et al. 2016, Mahoney et al. 2018); collectively, they can remove as much as 65% of a tree's seed crop
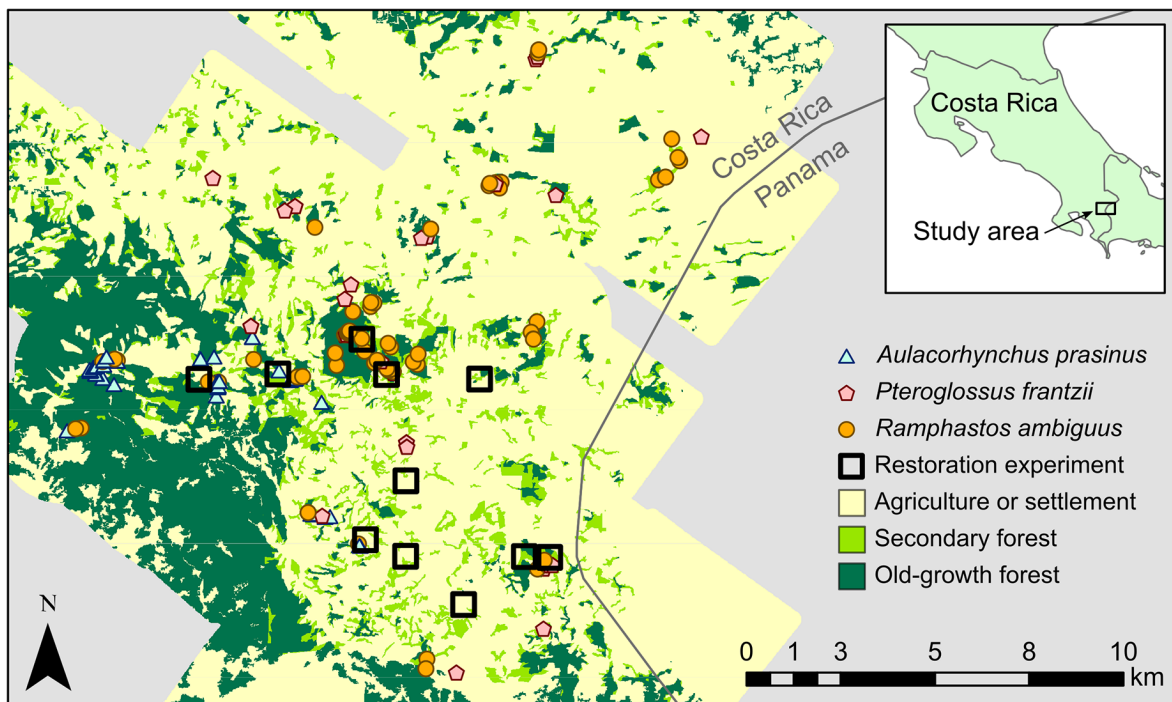
Fig. 1. Experimental sites, toucan detection locations, and land-use cover in the Coto Brus Valley of southern Costa Rica.

(Howe 1981). Despite being dependent on forest for nesting and foraging, they have the potential to fly long distances across open country, making them effective long-distance dispersal agents (Beltrán and Howe 2020). We excluded large-bodied Cracids (curassows, guans, and chachalacas), which are either not found (or very rarely found) in regenerating forests in the study area, or are not forest-dependent (e.g., the chachalaca *Ortalis cinereiceps*) and may be less likely to disperse forest tree seeds. We also excluded Psittacids (parrots and parakeets), which sometimes disperse viable propagules over long distances (Tella et al. 2015) and were often observed flying overhead, but were rarely observed in restoration sites. Finally, we excluded some large-bodied omnivores (e.g., the crake *Aramides cajaneus*) that occasionally eat fruit as part of a diet consisting primarily of invertebrates.

Toucan surveys

In 2011–2012, we quantified the occurrence of three toucan species in 55 forest fragments in our study region in order to develop habitat suitability models. The forest fragments represented two uncorrelated gradients in fragment size and forest cover within a 1000-m radius, stratified across elevation (Fig. 1). The area covered by a 1000-m radius approximates the upper range of home range sizes reported in previous studies (Graham 2001, Holbrook 2011, Kays et al. 2011). The fragments included the 49 fragments in Kormann et al. (2018), plus six additional fragments which we added to make the sample more balanced altitudinally. Fragments were selected according to a stratified-random design, based on aerial-based forest cover maps (2-m resolution; Hadley et al. 2014). A priori, we assigned fragments to a size class (small: <5 ha, large: >30 ha), and from both categories we selected fragments that represented a forest cover gradient (5–80%), included two elevational bands (880–1100 m asl and >1100–1500 m asl), and were spatially spread across the study area. Due to this selection procedure, all correlations between altitude, forest cover, and fragment size were low (all Pearson's $r < 0.5$).

We assessed toucan abundance using 50 m fixed-radius point counts and stopping rule-

based walkabouts, all performed by the same experienced observer (Jeisson Figueroa Sandí, JFS). Forest fragments were visited once between May and June (2011, 2012) in the early morning in a randomized order. Walkabouts lasted an average of 80 min in small fragments, and 155 min in large fragments. We performed 12-min point counts; three in each small fragment and six in each large fragment.

We also assessed toucan visitation three times per year (April–May, July–Aug, and November–December) in each of 11 restoration sites from 2010 to 2018 (Fig. 1). This monitoring was used to test habitat suitability model predictions and in turn predict large-seeded tree recruitment. Within each site, we actively searched each of three experimental plots for 20 min, walking along pre-established trails, and recorded when toucans were seen or heard within the plot. When possible, we also recorded the tree or plant species in which the bird was observed and its foraging and reproductive behavior. During each sampling effort, we visited sites and plots in random order. We made observations from 0600 to 0900 h during mild weather, including light fog or mist but excluding hard wind or rain. A single skilled observer (JAR) conducted all surveys in restoration sites.

Seedling surveys

In February to April 2017, RAZ and JAR comprehensively surveyed seven 50 × 50 m tree plantation restoration plots for LSAD tree species recruitment (Table 1). Species were classified as LSAD based on dispersal syndrome (zoochorous) and seed width (>10 mm; $N = 21$ species). We selected a 10-mm threshold for "large" seeds because this is approximately the maximum diameter that smaller birds such as tanagers and thrushes are capable of swallowing (Wheelwright 1985, Lindell et al. 2013). We selected all LSAD species rather than filtering for those with documented toucan dispersal because toucans characteristically have broad diets and the specific diets of toucans in our region have not been quantified (Wheelwright et al. 1984). All naturally recruiting individuals ≥10 cm in height were recorded in each plantation. We did not survey LSAD tree species recruitment in applied nucleation or natural regeneration treatment plots, largely due to the challenge of thoroughly

detecting all recruits within the dense grass cover found in parts of these treatments (Holl et al. 2018).

GIS variables

We used four local and four landscape-level environmental variables to build habitat suitability models for the three focal toucan species. At the local scale, we used the following: (1) elevation and (2) forest age (secondary vs. old-growth) at the point of occurrence; (3) the fragment area; and (4) the area of the fragment covered by old-growth forest. At the landscape scale, we used the area covered by forest irrespective of forest age within a buffer of (5) radius = 500 m and (6) radius = 1000 m around the point of occurrence. Further, we used the area covered by old-growth forest only within a buffer of (7) radius = 500 m and (8) radius = 1000 m around the point of occurrence.

Elevation was derived from a digital elevation model (EROS 2017). Orthophoto-based forest cover maps were derived from Hadley et al. (2014) (2-m resolution), and forest age was assigned using regional forest age classification maps based on aerial photography (Zahawi et al. 2015). We considered forest to be old-growth if it had been forested continuously from 1947 to 2015. We filled in forest age coverage gaps for about 10% of the study area using the Costa Rican National Forest Inventory (REDD/CCAD-GIZ-SINAC 2015).

Habitat suitability models

We determined the potential distribution for each toucan species in the study area by building species-specific habitat suitability models. These models used toucan data from our survey of 55 forest fragments but not observations from restoration sites. To characterize the ecological niche, we implemented a Bayesian presence-only approach (Maxent), to predict the likelihood of occurrence of a species by statistically comparing the environmental variables of locations where the species was observed, to randomly selected points from the study region (Phillips and Dudík 2008). Presence-only data have been criticized as having substantial sampling bias, such that species records are more likely to occur near areas that are more frequently visited by observers (Beck et al. 2014). We corrected for this potential bias through (1) our sampling design (stratified

Table 1. Large-seeded, animal-dispersed (LSAD) tree species censused in seven tree plantations in southern Costa Rica.

Species†	Family	IUCN‡	Growth form§	Seed size (mm)	Successional stage	Seedling density (ind./0.25 ha)		
						Min	Max	Median
Brosimum alicastrum Sw.	Moraceae	LC	CT	10–15	Both	0	1	0
Calophyllum brasiliense Cambess.	Calophyllaceae	LC	CT	10–15	Late	0	183	2
Drypetes brownii Standl.	Putranjivaceae	LC	CT	10–15	Late	0	109	0
Guarea bullata Radlk.	Meliaceae	LC	CT	10–15	Late	2	61	15
Guarea chiricana Standl.	Meliaceae	LC	UT	10–15	Late	0	14	0
Guarea glabra Vahl	Meliaceae	LC	UT	>15	Late	0	16	1
Nectandra purpurea (Ruiz & Pav.) Mez.	Lauraceae	NA	CT	10–15	Late	0	1	0
Nectandra reticulata (Ruiz & Pav.) Mez	Lauraceae	LC	CT	10–15	Late	0	24	1
Ocotea lentii W.C. Burger	Lauraceae	NA	CT	10–15	Late	0	14	0
Ocotea oblonga (Meisn.) Mez	Lauraceae	LC	CT	10–15	Late	0	39	0
Otoba novogranatensis Moldenke	Myristicaceae	NA	CT	>15	Both	1	36	11
Prunus occidentalis Sw.	Rosaceae	NA	CT	10–15	Late	0	10	0
Prunus sp.	Rosaceae	NA	CT	10–15	Late	0	4	0
Pseudolmedia mollis Standl.	Moraceae	NA	CT	10–15	Late	0	417	4
Ruagea glabra Triana & Planch.	Meliaceae	LC	CT	10–15	Late	1	57	16
Sloanea brenesii Standl.	Elaeocarpaceae	NA	CT	10–15	Late	0	15	0
Symphonia globulifera L. f.	Clusiaceae	LC	CT	10–15	Late	0	1	0
Trichilia pittieri C. DC.	Meliaceae	VU	CT	10–15	Late	0	8	0
Virola koschnyi Warb.	Myristicaceae	NA	CT	>15	Late	0	7	0
Virola sebifera Aubl.	Myristicaceae	LC	CT	10–15	Late	0	29	0
Virola sp.	Myristicaceae	NA	CT	10–15	Late	0	6	0

† Species taxonomy follows Tropicos.org.
‡ IUCN (2019) conservation status: Least Concern (LC), Vulnerable (VU), Not Assessed (NA).
§ Growth forms: Canopy tree (CT), Understory tree (UT).

random sampling) and (2) testing for potential sampling bias using a pairwise distance matrix to identify potential data clustering. However, we did not find any considerable spatial clustering for any of the species.

We developed a series of species-specific niche models at a 10×10 m spatial scale. We used occurrence points of the species and a total of 1500 random points from the rest of our study area to define the background to model the likelihood of species occurrence. Following recent discussion regarding model complexity within Maxent models, we estimated optimal complexity using several regularization multipliers and combination of feature classes (Warren and Seifert 2011). We optimized model complexity for every species separately by running 12 Maxent models per species, while permuting both the regularization multiplier and combinations of

the used feature classes. We implemented three feature class options (i.e., linear, linear and quadratic, and linear/quadratic/product) and four regularization multipliers (i.e., 0.5, 1.5, 2.0, and 2.5) using the ENMeval package for R (Muscarella et al. 2018). AUC is a commonly applied measure of the goodness-of-fit for distribution models and ranges from 0.5 for poorly performing models to 1.0 in perfectly fitting models. We used AUC to test model performance through a cross-validated masked checkerboard subset of randomly selected occurrence records and ensured that the models selected where above 0.7 (Radosavljevic and Anderson 2014, Muscarella et al. 2018). Habitat suitability was estimated for the centroid of each restoration site, using the best model for each toucan species. For landscape variables (e.g., forest cover), the habitat suitability estimate included the restoration sites,

which made up <1% of the total area within a 500 m radius buffer.

Data analysis

We used linear and general linear models to analyze correlations among estimated habitat suitability, toucan detections in restoration sites, and the richness of LSAD tree recruits in tree plantations. Specifically, we predicted the richness of LSAD tree recruits (response variable) as a function of estimated habitat suitability for each toucan species and, in separate models, the number of detections of each toucan species in restoration sites. We also used toucan habitat suitability to predict the number of toucan detections in restoration sites. For each analysis, we compared linear models and general linear models with Poisson error; the best fit is reported. We tested for overdispersion and found none (Cameron and Trivedi 1990). We tested for spatial autocorrelation in toucan detections in restoration sites using Mantel tests. Goodness-of-fit was calculated as a pseudo-R^2: $1 -$ (residual deviance/null deviance). Sample size was $N = 11$ for analyses predicting toucan detections and $N = 7$ for analyses predicting LSAD tree recruitment richness in plantation plots. *Aulacorhynchus* was excluded from LSAD tree recruitment richness analyses because only one tree plantation that was censused for LSAD tree recruits also had an *Aulacorhynchus* detection. Detections of *Pteroglossus* and *Ramphastos* were somewhat correlated (pseudo-$R^2 = 0.24$, $P = 0.079$), so they were not used as predictors in the same model.

To test whether rarer seedling species were more likely to be found in plantations where toucan habitat suitability was greater, we used a generalized linear mixed model with binomial error and a random, variable-intercept term for site (lme4 package; Bates et al. 2019). We defined rare species as those detected in fewer than half of plantations.

To test whether communities of LSAD tree recruits were nested, with species in less-diverse communities forming subsets of the species in more diverse communities, we used the method proposed by Almeida-Neto et al. (2008), implemented in the vegan package in R (Oksanen et al. 2019). This method produces a statistic, NODF (No Overlap and Decreasing Fill) ranging from 0 to 100, with 0 indicating a non-nested pattern and 100 indicating a perfectly nested pattern. We tested the likelihood that the observed value of NODF was produced by chance by comparing it to simulated communities (R00) with equivalent fill (i.e., the same number of presences assigned non-sequentially) but potentially different column and row frequencies.

Data and code underlying these analyses are available from Dryad. Statistical analyses were performed in R version 3.6.1 (R Development Core Team 2019).

RESULTS

Toucan habitat suitability

During our toucan surveys in the 55 forest fragments, we observed a total of 45 *Aulacorhynchus prasinus*, 44 *Pteroglossus frantzii*, and 69 *R. ambiguus* detections. The models for all species performed well when tested on randomly selected samples (Appendix S2). The best model for *Aulacorhynchus* had AUC of 0.98; *Pteroglossus* had AUC of 0.75; and *Ramphastos* had AUC of 0.83 (Appendix S1: Table S3). Models with the lowest AIC were maintained. Toucan species selected divergent habitat types based on elevation, and the age and extent of forest cover at various spatial scales (Fig. 2). The smallest toucan, *Aulacorhynchus*, selected high-elevation forests, without any strong selection of age or amount of forest at any spatial scale (Fig. 3). The largest, *Ramphastos*, selected mid-elevations, areas with higher amount of total forest at the point of occurrence, and areas with more old-growth forest within a 500-m radius. *Pteroglossus* selected mid-elevational secondary forests—avoiding larger mature forest fragments most strongly at a scale of 1000-m radius (Fig. 3). Estimated habitat suitability for the restoration sites ranged from 0.00 to 0.39 for *Aulacorhynchus* given its restricted high-elevation range (mean 0.08), 0.08–0.85 for *Pteroglossus* (mean 0.40), and 0.13–0.84 for *Ramphastos* (mean 0.48).

Toucan detections in restoration sites

We detected a total of 27 toucans within the 11 restoration sites (8 *Aulacorhynchus*, 13 *Pteroglossus*, 6 *Ramphastos*) during 296 hours of observation over 8 yr. The two smaller toucan species were detected 1 yr earlier in plantations
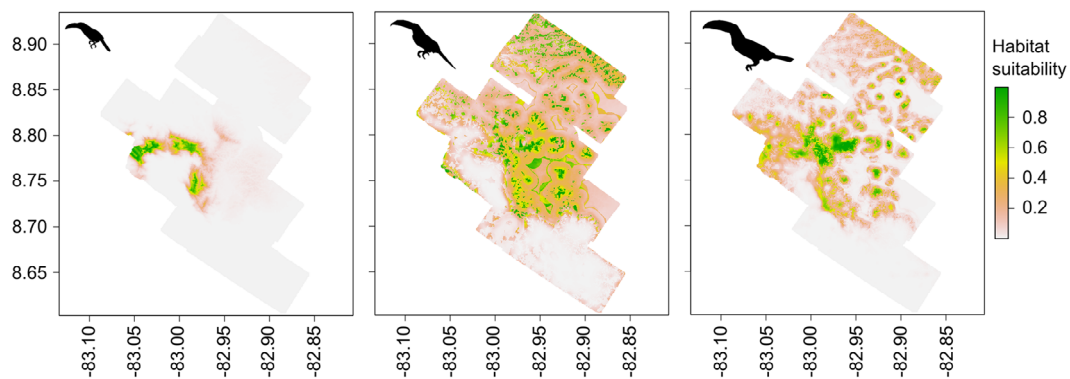
Fig. 2. Estimated habitat suitability for three sympatric toucans in southern Costa Rica. From left to right: *Aulacorhynchus prasinus*, *Pteroglossus frantzii*, *Ramphastos ambiguus*. Axes denote latitude and longitude.
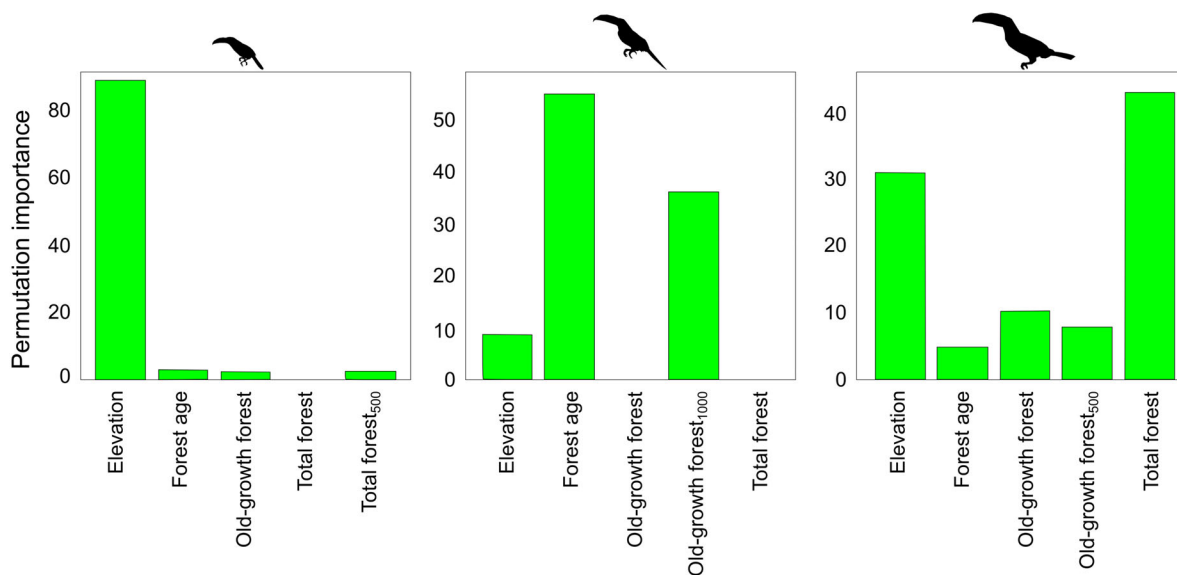

Fig. 3. Permutation importance of all environmental variables in the final habitat suitability models for three sympatric toucans in southern Costa Rica. From left to right: *Aulacorhynchus prasinus*, *Pteroglossus frantzii*, *Ramphastos ambiguus*. Subscripted numbers denote the radius (m) at which forest cover was measured.

compared to applied nucleation and 5–6 yr earlier in plantations compared to natural regeneration (Fig. 4). The largest toucan species, *Ramphastos*, was detected later than the other two species and was only detected in plantations. Toucans were most often observed perching on tree branches and less often foraging on fruits (*Aulacorhynchus, Pteroglossus*) or insects (*Ramphastos*; Appendix S1: Table S4). *Aulacorhynchus prasinus* detections were spatially autocorrelated

with 90% of detections concentrated in the two highest elevation sites (Mantel $r = 0.34$, $P = 0.025$; Appendix S1: Table S5).

Toucan detections and predicted habitat suitability in restoration sites

Toucan detections in restoration sites increased with increasing estimated habitat suitability for two of the three toucan species (Fig. 5). Habitat suitability constructed from an independent
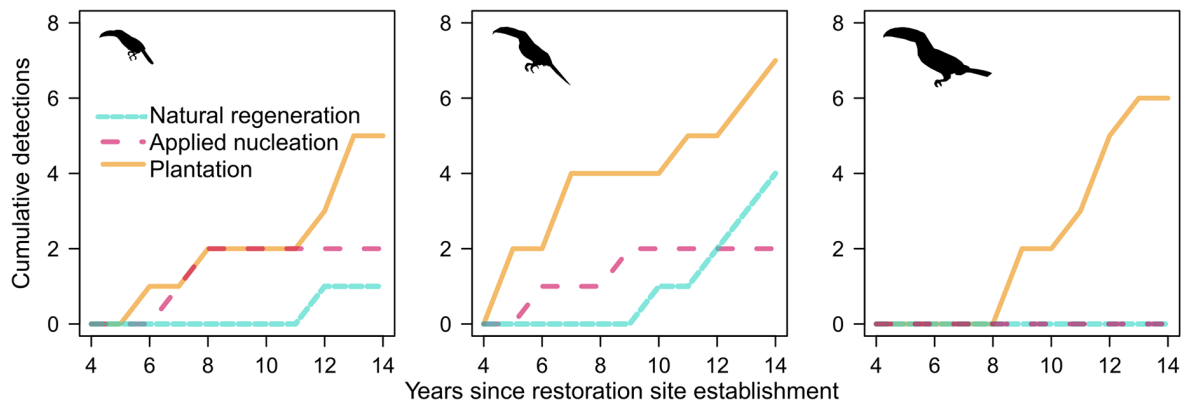
Fig. 4. Cumulative detections of three toucan species across 11 tropical forest restoration sites in southern Costa Rica (2010–2018). From left to right: *Aulacorhynchus prasinus, Pteroglossus frantzii, Ramphastos ambiguus.*

dataset explained 99% of variance in *Aulacorhynchus* detections ($P < 0.001$) and 58% of variance in *Ramphastos* detections ($P = 0.004$) in restoration sites. *Pteroglossus* detections were not related to estimated habitat suitability. When flyovers were excluded, trends were similar but dampened (Appendix S1: Fig. S2).

Richness of large-seeded, animal-dispersed (LSAD) tree recruits

The species richness of LSAD trees recruiting into plantations ranged from 4 to 14 (median 12; Table 1). *Ramphastos* habitat suitability explained nearly 2× more variance in LSAD richness compared to the number of *Ramphastos* detections in the restoration sites (pseudo-$R^2 = 0.87$ for habitat suitability vs. 0.47 for toucan detections; Fig. 6), whereas estimated *Pteroglossus* habitat suitability was unrelated to LSAD species richness. LSAD richness was 2–3× greater in tree plantations where *Pteroglossus* or *Ramphastos* toucans were detected compared to plantations where no toucans were detected (Fig. 6). When flyovers were excluded, trends were similar but weaker (Appendix S1: Fig. S3).

LSAD richness also correlated with landscape tree cover within 500 m (Appendix S1: Fig. S4). Compared to the best models using toucan
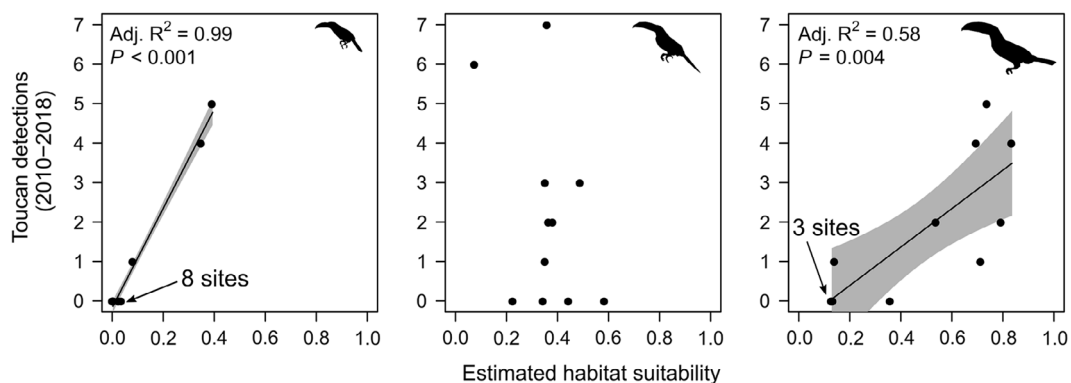

Fig. 5. Correlation between estimated habitat suitability and toucan detections in tropical forest restoration sites in southern Costa Rica ($N = 11$). Toucan detections in all restoration treatments are included. From left to right: *Aulacorynchus prasinus, Pteroglossus frantzii,* and *Ramphastos ambiguus.* Adj. R^2 is calculated with linear regression. Solid lines depict model fits with $P < 0.05$. Gray shading indicates 95% confidence interval.
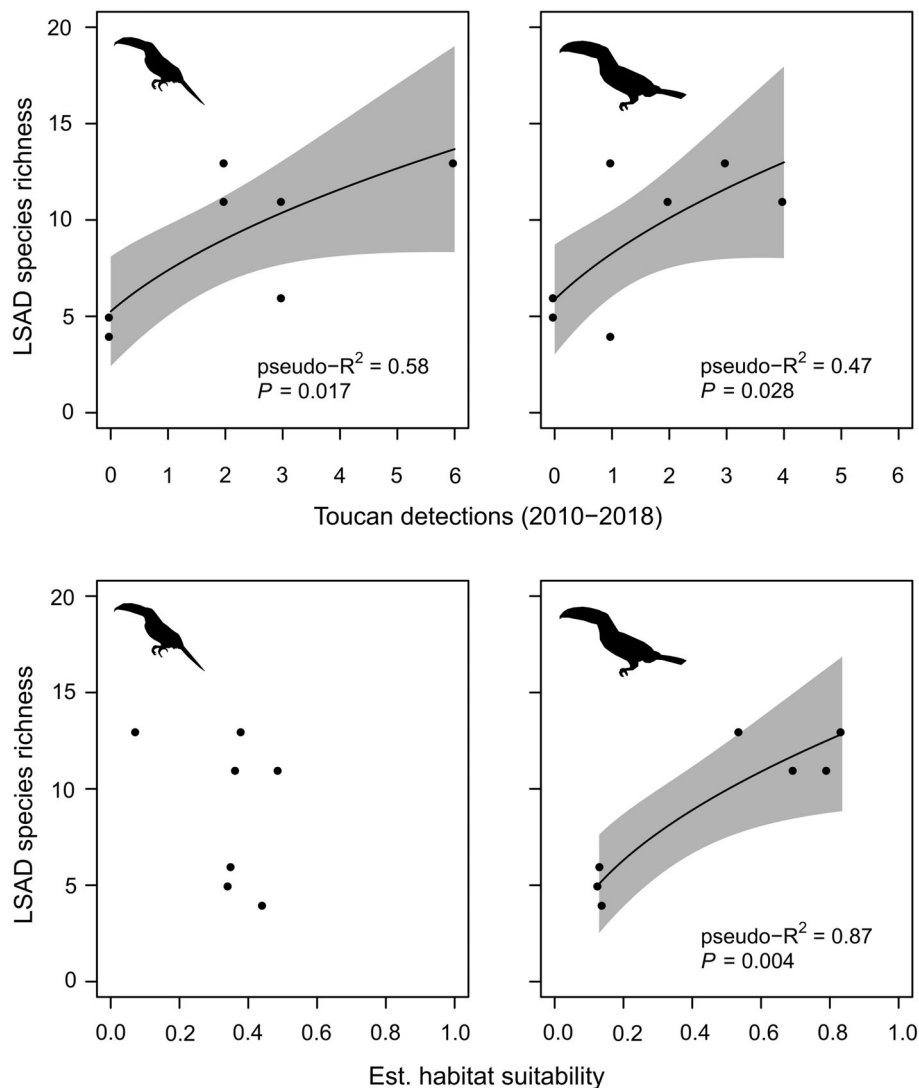
Fig. 6. Correlations between the richness of large-seeded, animal-dispersed (LSAD) tree seedlings recruiting into restoration plantations and the number of toucan detections in restoration sites (top row) or the estimated habitat suitability (bottom row). Left-hand panels show *Pteroglossus frantzii*; right-hand panels show *Ramphastos ambiguus*. *Aulacorhynchus prasinus* is not shown because there was only one observation in a site that was also surveyed for LSAD seedlings. Model fit estimated with GLM using Poisson error and log-link. Goodness-of-fit is reported as $1 - ($residual deviance/null deviance; "pseudo-R^2"). Solid lines depict model fits with $P < 0.05$. Gray shade indicates 95% confidence interval. $N = 7$ restoration plantations.

detections or estimated habitat suitability, landscape tree cover predicted only 59% and 30% as much variance, respectively.

Nested LSAD recruit community structure

Seventy-one percent of LSAD tree species (15/21) were found only in sites with estimated

Ramphastos habitat suitability of at least 0.5 (Fig. 7). Also, plantations with high *Ramphastos* habitat suitability had more rare seedling species, that is, species detected in <4 plantations ($z = 3.726$, $P = 0.0002$). Fourteen species were rare; of these 14 rare species, 13 were found only in plantations where *Ramphastos* habitat suitability was
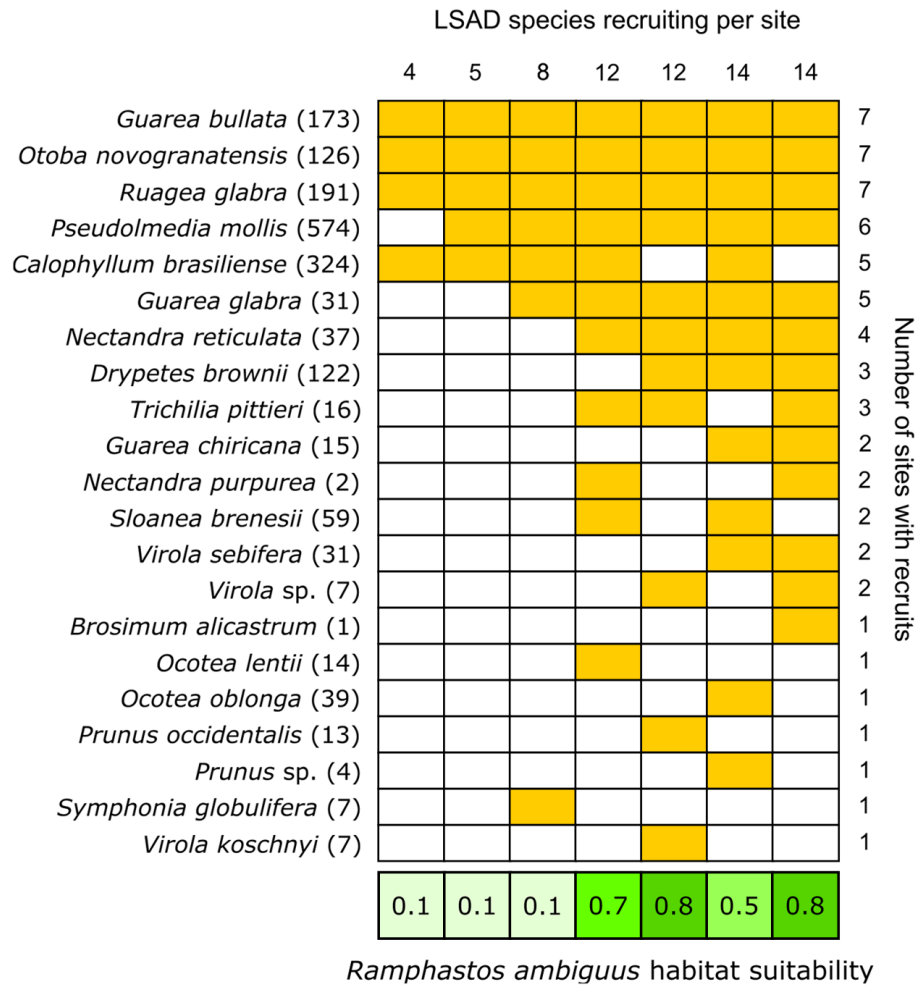
Fig. 7. Nestedness of LSAD species recruitment in seven tree plantations. Sites (columns) are sorted in ascending order by the number of LSAD species recruiting. Species (rows) are sorted in descending order (top to bottom) by the number of sites where they were observed recruiting. Sample sizes (number of individuals) are shown in parentheses for each species. Estimated habitat suitability for *Ramphastos ambiguus* is shown at the bottom for each site. Note that 13 out of 14 rare LSAD species (detected on ≤3 sites) occurred only on sites with estimated habitat suitability for *Ramphastos ambiguous* ≥0.5, and 7 only when habitat suitability was ≥0.7.

≥0.5, and 7 were found only when habitat suitability was ≥0.7. Communities of recruiting LSAD species were incompletely nested (NODF = 0.66, $P = 0.01$), with species in less-diverse tree plantations often but not always forming nested subsets of species in more diverse plantations.

DISCUSSION

Seminal reviews on the state of restoration ecology highlight the need to understand spatial dependencies (Suding 2011), particularly those that bridge the relevant spatial scales of plants and animals (McAlpine et al. 2016). Prior studies demonstrate that many animals, including toucans, select habitat at two spatial scales, first choosing a suitable landscape and then moving selectively within that landscape (Orians and Wittenberger 1991, Graham 2001). Likewise, our results support a conceptual model across multiple spatial scales for predicting toucan-mediated dispersal of large-seeded, animal-dispersed

(LSAD) trees during tropical forest restoration (Fig. 8). At a landscape scale (hundreds of meters), the largest toucan in our study area, *R. ambiguus*, selected habitat based on forest cover and elevation. At a local scale (tens of meters), *R. ambiguus* selectively visited seven 15-yr-old tree plantations within suitable habitat, but visits to adjacent plots restored via natural regeneration or applied nucleation were not detected. As a result, LSAD tree colonization was 2–3× richer, and included more rare species in tree plantations within suitable toucan habitat compared to tree plantations outside of suitable habitat.

Habitat suitability models for the three toucans generally followed expectations based on prior literature. *Ramphastos ambiguus* and *Pteroglossus frantzii* selected landscapes with greater forest cover, consistent with earlier classifications of these species as moderately forest-dependent (Stiles 1985, Lindell et al. 2004). *Aulacorhynchus*

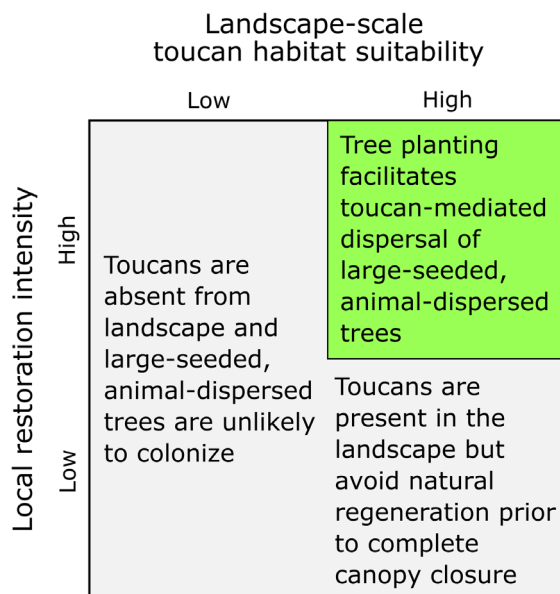## Landscape-scale toucan habitat suitability

Fig. 8. Conceptual model of the two interacting spatial scales that shape the success of animal-assisted forest restoration. Toucan-mediated seed dispersal is only likely in the green quadrant where both the landscape context and local restoration actions facilitate toucan-mediated dispersal for large-seeded trees. Restoration efforts in the gray zone are unlikely to facilitate toucan-mediated seed dispersal either because toucans are absent from the landscape or because they avoid the local site.

prasinus selected high-elevation habitat, typically above 1400 m in our study region. Previous observations suggest that within its higher elevation habitat, *A. prasinus* also inhabits forest, or at least areas with scattered trees (Stiles and Skutch 1989). For two out of the three species, habitat suitability models were supported by strong correlations with independent observations within restoration sites. This was not the case for *P. frantzii*. The lack of congruity between modeled habitat suitability and observations of *P. frantzii* in restoration sites suggests that the forest fragment data underlying the habitat suitability models do not completely represent the diverse habitat affinities of this species. Although *P. frantzii* nest in trees, we regularly observed them foraging in fruiting trees well outside of forest, as have others (Arias-Campos 2015).

Within suitable landscapes, toucan activity was greater in areas with active forest restoration via tree planting than in areas undergoing natural regeneration. Tree planting may attract birds by providing high perches, shade, cover from diurnal predators, and food in the form of fruits or insects (Morrison et al. 2010). However, tree plantings in our study did not incorporate fleshy-fruited species except for *Inga edulis*, which produces an indehiscent pod filled with sweet pulp, but is difficult for birds to open and which we never observed birds eating. Toucans did, however, feed on fruits of small-seeded tree species that recruited naturally into the restoration sites. We also observed toucans hunting insects in tree plantations—a behavior that was previously reported for a related toucan, *R. sulfuratus*, in a tree plantation in Mexico (Davlantes and Howe 2018).

Both direct toucan observations and estimated toucan habitat suitability were associated with greater LSAD species richness within tree plantations. The best predictor was habitat suitability for *R. ambiguus*, estimated from a model using an independent set of observations. Ours is one of several studies recommending habitat suitability modeling of species or communities to inform decisions about where to restore or conserve habitat (e.g., Burnside et al. 2002, Nekhay et al. 2009, Questad et al. 2014, Tomlinson et al. 2018, Zárrate-Charry et al. 2018), but one of the few to show that habitat suitability models can actually predict species interactions and affect forest

recovery rates. The fact that *R. ambiguus* habitat suitability predicted LSAD species recovery in tree plantations suggests that this toucan is an effective restoration agent (sensu Beltrán and Howe 2020), that is, a seed disperser capable of dispersing large seeds into regenerating forests. Indeed, more than two-thirds of LSAD species recorded in tree plantations were found only in sites where *R. ambiguus* was observed. *Ramphastos ambiguus* is 3–4× larger than the other toucans in this study; its greater size could indicate a greater capacity for dispersing more and larger seeds over longer distances (Kays et al. 2011). Moreira et al. (2017) likewise concluded that *R. ambiguus* maintains seed dispersal processes for an LSAD species (*Virola surinamensis*) in human-dominated landscapes in lowland southern Costa Rica. A rule of thumb may be that if large toucans are observed near a restoration site, that site is likely to attract natural recolonization of large-seeded species provided that restoration actions create suitable local habitat structure.

It is important to note that we did not do a census of LSAD recruitment in natural regeneration or applied nucleation plots for this study. Whereas our results suggest that toucan-mediated seed dispersal should be greater in plantations than other restoration treatments, we did not explicitly test that hypothesis here. Data from smaller permanent vegetation sampling quadrats within our experimental plots indicate that LSAD tree seed dispersal (seeds·m^{-2}·yr^{-1}) and seedling recruitment (seedlings/m^2) are similarly abundant in plantations and applied nucleation; both are an order of magnitude greater than in natural regeneration (Holl et al. 2017). Accordingly, LSAD species recruitment in applied nucleation could be the result of seed dispersal by *Pteroglossus*, Phyllostomid bats, or other large frugivores that we did not include in this study.

Our conclusions may extend to other tropical forest regions with the following limitations. First, toucan habitat models may be less accurate when applied to regions with different agricultural matrices or with greater persecution of toucan populations (Holbrook and Loiselle 2009). Trees cover approximately 30% of our study area, and much of the regional tree cover consists of fence rows and isolated trees in a matrix of small farms (Mendenhall et al. 2011, Zahawi

et al. 2015). In contrast, large, industrialized regions have sharper matrix contrast (e.g., when sugarcane plantations border forests), and toucans may be more restricted within larger forest fragments (Sodhi et al. 2004, Galetti et al. 2013).

Also, while toucans are considered important seed dispersers in neotropical forest restoration contexts, key seed dispersers vary geographically (Beltrán and Howe 2020). Given the effort required to make relatively few direct toucan observations in our restoration sites, we hope that researchers and practitioners in other regions can create and interpret habitat suitability models directly instead of making painstaking observations of hornbills, cassowaries, lemurs, or other regionally important frugivores using restoration sites (Mack 1995, Lenz et al. 2011, Razafindratsima and Dunham 2014). We also encourage further research on how restoration interventions influence frugivore movements via changes to landscape configuration and composition (Metzger and Brancalion 2016). For example, wooded corridors, rope bridges, and diversified agroecological matrices may facilitate movements for forest-dependent LSAD dispersers from seed sources to restoration sites (Jesus et al. 2012, Hernández-Pérez 2015, Kormann et al. 2016, Perfecto et al. 2019).

For land managers, the conceptual model supported by our data implies, first, that tree planting can catalyze toucan-mediated dispersal of large-seeded plant species when restoration projects fall within suitable toucan habitat. Planting tree species that produce toucan-preferred fruits could further amplify this effect (Howe 2016). When restoration sites fall outside of toucan habitat, managers will need to introduce more LSAD plant species to reach the same diversity level. Second, contemporary landscape restoration initiatives should aim to restore forest at scales that could transform non-habitat to habitat for large toucans (Dave et al. 2019). Restoring toucan habitat will increase biodiversity resilience at larger scales because subsequent restorations will benefit from toucan-mediated dispersal services. That said, the plant species that toucans subsequently disperse will depend on the seed source availability in the landscape, which itself will depend on the species retained in the agricultural landscape or established during landscape restoration. An important issue is that

LSAD species often take a long time to fruit and may be logged before they reach maturity (Martínez-Garza and Howe 2003). Third, natural regeneration is often heralded as a viable restoration strategy (Crouzeilles et al. 2020), but leaving a site to regenerate without intervention is unlikely to recover significant toucan-mediated seed dispersal within the first decade of recovery, at least in agriculturally dominated landscapes comparable to the one studied here.

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Data Availability

Data are available from Dryad: https://doi.org/10.7291/D14T2W

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3868/full